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The giant devil ray *Mobula mobular* (Bonnaterre, 1788) is not giant, but it is the only spinetail devil ray

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Abstract

Mobula mobular, a mobulid species once considered a Mediterranean Sea endemic, has received its common name "giant devil ray" based on repeated misidentifications of oceanic manta rays, *Mobula birostris*, that had strayed into the Mediterranean, where they had never been reported from before. Based on the maximum known size (350 cm disc width) of *M. mobular,* when compared to some of its congenerics, the giant devil ray is not giant at all. A recent revision of the phylogeny and taxonomy of genus *Mobula*, which included, amongst other things, the decision to consider the circumtropical spinetail devil ray *M. japanica* a junior synonym of *M. mobular*, has caused the latter species to become circumglobal, and the only known mobulid with a tail spine. As a consequence, it is here recommended that the common name of *M. mobular* be "spinetail devil ray".

Keywords: Mobulids, Manta, Fish nomenclature, Taxonomic misidentification

Background

Understanding the correct taxonomy of manta and devil rays (*Mobula* spp.) has remained challenging since the initial description of the first two species within the monotypic family Mobulidae in the late eighteenth century (Bonnaterre, 1788; Walbaum, 1792). Nomenclatural confusion has persisted for centuries, exacerbated by inadequate reports and identifications of mobulid species across the world's oceans (Notarbartolo di Sciara, 1987). As a consequence, many descriptions were not placed into a wider taxonomic context, preventing the accurate determination of the range extent of the different species, and resulting in the attribution of a plethora of different names to the same species (Notarbartolo di Sciara, 1987). Confounding this issue for mobulids is: a) the subtle morphological differences amongst species of *Mobula*, b) the poor representation of mobulid specimens in museum collections, often due to their large size, and c) limitations to the heuristic process intrinsic to pre-digital zoological investigations. As for all early taxonomic endeavours, the learning process was hindered by a lack of supporting genetic insight, by the unavailability of photographic documentation, and by slow and intermittent communications, which caused most ichthyologists to work in isolation.

Conditions have dramatically improved in recent decades as a result of significant scientific and technological advances that combine to enable precise and unambiguous morphological documentations. The scientific advancement of genomic investigations has also led to the streamlining of taxonomy with phylogenetics, often re-shaping our assessments of species classifications as a result (Wiley & Lieberman, 2011). Finally, the immersion of investigators in a collective medium, facilitated by the Internet, has also allowed unprecedented opportunities for comparisons, communication, and collaboration. As a consequence, our understanding of the taxonomic status of mobulids has improved considerably in the past decade, with the reorganisation of the family into a configuration reflecting our increasing understanding of the species' phylogenies (Adnet et al., 2012; Poortvliet et al., 2015; White et al., 2017; Hosegood et al., 2018).

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The ramifications of the original taxonomic confusion affecting this ray family continue to persist. Therefore, clarity is required if the correct research conclusions and effective conservation efforts are to be achieved. Until recently, one such area of confusion surrounded the giant devil ray, *Mobula mobular* (Bonnaterre, 1788), a Mediterranean species, and the circumtropical spinetail devil ray, *Mobula japanica* (Müller & Henle, 1841). Many morphological traits shared by *M. mobular* and *M. japanica* (such as colour, shape of teeth, position of spiracles, presence of a tail spine, and tail length) set these species apart from other *Mobula* (Notarbartolo di Sciara, 1987). Until the revision by White et al. (2017), *M. mobular* was considered to be distinct from *M. japanica* largely due to the purported significantly larger size of the former, said to reach a disc width (DW) in excess of 5 m (Bigelow & Schroeder, 1953). In addition, evidence of minor morphological and morphometric differences was recognised between the two (Notarbartolo di Sciara, 1987). On such bases, recommendations were made to keep the two taxa provisionally separate, pending further investigations (Notarbartolo di Sciara, 1987; Adnet et al., 2012; Poortvliet et al., 2015). As a consequence of such uncertainties, the difficulty of distinguishing *M. mobular* from *M. japanica* also resulted in confusion about their respective ranges, with the former having been frequently reported outside of the Mediterranean Sea in various North Atlantic locations; such as Ireland, Portugal, Madeira, the Canary islands, West Africa (from Morocco to Senegal), and even Cuba (Notarbartolo di Sciara, 1987). Conversely, *M. japanica* was reported in the Mediterranean (Rafrafi-Nouira et al., 2015; Capapé et al., 2015; Sakalli et al., 2016). For this reason, several authors recommended that the determination of the ranges of these two nominal species be placed on hold pending a clarification of their taxonomical relationship (Notarbartolo di Sciara, 1987; Notarbartolo di Sciara et al., 2015; Abudaya et al., 2017).

Recently, the contribution by molecular methods to taxonomic investigations have provided strong evidence in support of the two taxa being a single species (Poortvliet et al., 2015; White et al., 2017; Hosegood et al., 2018). This caused *M. japanica* to become a junior synonym of *M. mobular*, the latter resulting in a circumglobal species. However, this new configuration still leaves unresolved the matters of the size and morphological differences between the two formerly recognised taxa. Here, we intend to address these matters and assess their substantiation; with the intent of disputing the widely reported notion that *M. mobular* is a giant of its kind, and asserting that it is the only spinetail devil ray.

Sizeable mistakes

The type description of *Raja mobular* (= *Mobula mobular*) by P. J. Bonnaterre in 1788 is based on an earlier description by H.L. Duhamel du Monceau (1782), who reported on a specimen captured in a fixed tuna trap near Marseille (France) in 1723, with a DW just under 5 m (~ 6 ft. for each "wing", and 3 ft. 10 in for the trunk between).

Two additional reports also purported the notion that *M. mobular* attains a gigantic size. The first of these is a communication by Pellegrin (1901), reporting on the capture near Oran (Algeria) of a huge ray, "*appartenant très probablement à l'espèce méditerranéenne* Dicerobatis giorna" (= *M. mobular*), having a DW of 5.2 m and a weight of 900 kg, but with no further details offered. Pellegrin (1901) also mentioned the capture in 1898 of another ray, about 5 m wide ("*mesurant monté 5 mètres environ*") in the Bay of Rosas on the Mediterranean coast of Spain, acquired by the National Museum of Paris. The presence of this stuffed specimen (MNHN 1899–1) in the Paris Museum, labelled as *M. mobular*, was confirmed in 1987 by B. Seret (*in litteris*) to be a female *Mobula birostris* (Bancroft, 1829) with a DW of approximately 470 cm.

A fourth instance of a very large mobulid from the region involved a ray captured in September 1916 in the Gulf of Cadiz (Spain), just outside of the Mediterranean Sea. That specimen, with a DW of 4.55 m and a weight of 358 kg, was identified as *M. mobular* by Lozano Rey (1928). However, based on Lozano Rey's description and published photograph (Fig. 1), it can be concluded that this Cadiz specimen was in fact *M. birostris* for the following reasons. First, the reported mouth width ("*90 cm de anchura de boca*"), equalling 19.8% of the ray's DW, is much larger than the mouth width of *M. mobular*, reported as 11.9% DW (coefficient of variation based on samples of *M. mobular* and *M. japanica* = 3.9) by Notarbartolo di Sciara (1987), but is consistent with the metric for *M. birostris* (Marshall et al., 2009). Second, the distinctive dorsal white shoulder markings clearly visible in the photograph in Lozano Rey's report are typical of *M. birostris* (Fig. 1a-b) (Stevens et al., 2018), yet quite different from the thick dark band which stretches from eye-to-eye on the nuchal region of *M. mobular* (Fig. 1c) (Stevens et al., 2018). Third, the length of the unfurled cephalic fins of the Cadiz specimen is consistent with that of *M. birostris* (Fig. 1a-b). Finally, the eyes of this specimen protrude from the contours of the animal's head, like in *M. birostris* (Fig. 1a-b), in contrast to *M. mobular* (Fig. 1c).

The sizes of the four specimens mentioned above all greatly exceed the maximum size of *M. mobular* reported in recent decades from a variety of sources across multiple localities. For example, in a sample of 274 *M. mobular* of both sexes, many of which were sexually mature, captured off Gaza (Palestine) between 2014 and 2016, the maximum recorded DW was 320 cm (mean = 273 cm, range 173–320 cm) (Abudaya et al., 2017). Reliable measurements of specimens of *M. mobular* captured in the Mediterranean Sea over the past few decades (e.g., Notarbartolo di Sciara and

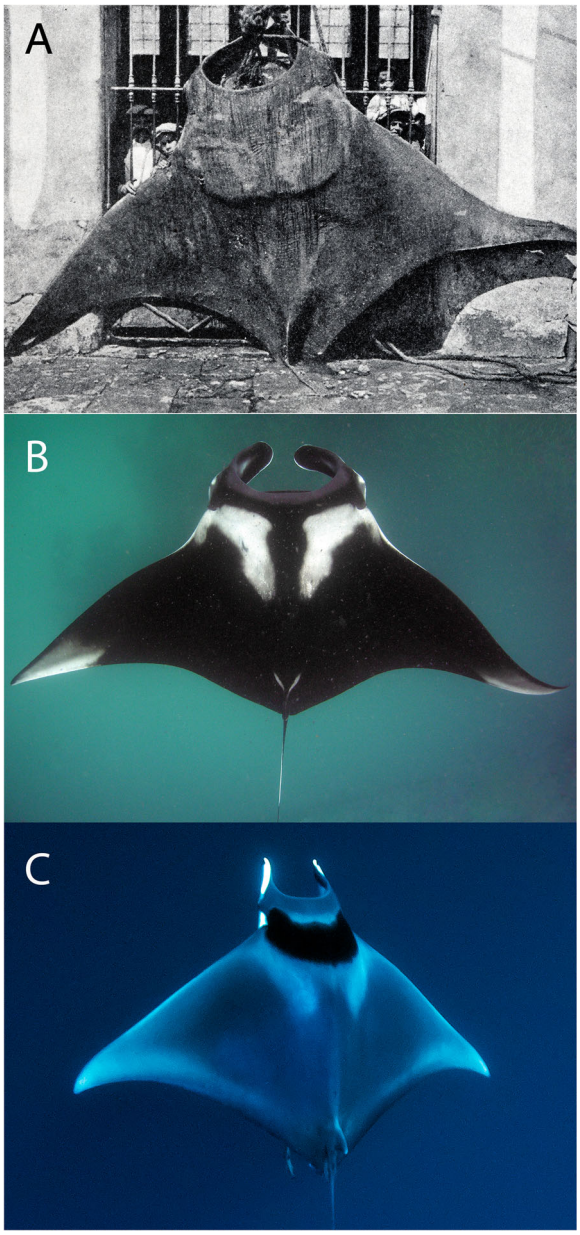

Fig. 1 a A specimen of *Mobula birostris* measuring 455 cm DW, landed in Cadiz, Spain in 1916, and identified as *Mobula mobular* (Lozano Rey 1928). Reprinted with permission from the Museo Nacional de Ciencias Naturales, Madrid. **b** *M. birostris* from the Maldives (© Guy Stevens, The Manta Trust). **c** *M. mobular* from California, US (© Mike Couffer)

Serena, 1988 ; Bradai & Capapé, 2001; Hemida et al., 2002; Celona, 2004; Scacco et al., 2008; Bello et al., 2012; Holcer et al., 2012) never provided DW sizes exceeding 350 cm; the latter having been reported by Storai et al. (2011) from a tuna trap in southwestern Sardinia. The measured sizes of *M. mobular* from the Mediterranean Sea are, in fact, consistent with the maximum reported size of 310 cm DW for *M. japanica* (= *M. mobular*) in New Zealand (Paulin et al., 1982). Notarbartolo di Sciara (1987) noted that the maximum size in this species may vary between populations. Indeed, in a sample of 78 specimens from the Gulf of California, many of which were sexually mature, no individual reached a DW of 240 cm (Notarbartolo di Sciara, 1988).

Given that no accurately measured *M. mobular* has ever exceeded a DW of 350 cm, combined with the aforementioned misidentification ascertained through the photograph published by Lozano (1928), it can be presumed that the specimens mentioned by Duhamel du Monceau (1782) and Pellegrin (1901), having DWs of 483 and 520 cm, were not *M. mobular*, but instead *M. birostris* (Table 1).

Morphological, morphometric and genomic aspects

Most diagnostic characteristics of *M. mobular* fully coincide with those formerly delineated for *M. japanica*, and in their combination set it apart from other *Mobula* species. These characteristics include: colouration, peg-like teeth, the longest tail of all *Mobula* (with a series of denticles running longitudinally on both sides), slit-like spiracles situated dorsally to the plane of the pectoral fins, a spine at the base of the tail, and the morphology of the branchial filter plates (Notarbartolo di Sciara, 1987; Stevens et al., 2018). However, some morphological, morphometric and genetic differences between the two taxa exist. Adnet et al. (2012) argued for the validity of the species' separation on the basis of tooth morphology, although they admitted that dental differences are tenuous. Proportional dimensions indicate the absence of major differences between the two taxa, except DW, which is 10–14% greater in Mediterranean Sea specimens (see Additional File 1 for details), conferring to rays from this region a broader appearance. Finally, Bustamante et al. (2015), comparing the two taxa's mitogenomes, suggested the existence of a sister-cryptic species complex with very limited divergence (> 99.9% genetic identity), which could be explained as the result of a geographically and numerically restricted population of *M. mobular* within the Mediterranean Sea. Indeed, the presence of population structuring within this circumglobal species, with minor differentiation between the Indian/Pacific and Atlantic/Mediterranean geographical populations (Hosegood et al., 2018), can be ultimately reflected into the observed phenotypic differences, and should not be surprising.

Conclusions

Having ascertained that two of the gigantic mobulids misidentified as *M. mobular* (the Rosas and the Cadiz specimens) were oceanic manta rays *M. birostris*, we propose that the Marseille and Oran rays were also *M.*

Table 1 Large specimens, presumed or confirmed as *Mobula birostris,* originally identified *as M. mobular* between 1723 and 1916 (see text for references)

Originally identified	DW (cm)	Location	Year	Presumed (P) / Confirmed (C)
Mobula mobular	483	Marseilles, France	1723	*Mobula birostris* (P)
Mobula mobular	470	Bay of Rosas, Spain	1898	*Mobula birostris* (C)
Mobula mobular	520	Oran, Algeria	1901	*Mobula birostris* (P)
Mobula mobular	455	Cadiz, Spain	1916	*Mobula birostris* (C)

DW Disc Width

birostris that had strayed into the Mediterranean Sea. Other records exist of *M. birostris* straying north of its normal range in the Atlantic, including off New England (U.S.), Georges Bank (U.S./Canada), and Madeira and the Azores (Portugal) (Bigelow & Schroeder, 1953; Sobral & Alfonso, 2014). The occurrence of *M. birostris* within the Mediterranean Sea has never previously been recorded. Therefore, the specimen captured off Rosas and conserved in the Paris Museum Is the first confirmed record of this species in the region.

Our suggestion, that the specimen on which Bonnaterre (1788) based the type description of *Mobula mobular* was presumably a *M. birostris,* raises a taxonomic complication that we do not wish to pursue for the sake of nomenclatural stability. The level of uncertainty contained in ancient, second-hand reports involving measurements of such large specimens should also be considered.

Based on all currently available sources, we recommend that the maximum size of *M. mobular* reported in the literature be scaled down to 350 cm DW. We also consider that the species' common name of "giant devil ray" is no longer justifiable when placed into perspective with the much larger maximum sizes of its congenerics, the oceanic manta ray *M. birostris* (680 cm DW) and of the reef manta ray *M. alfredi* (450 cm DW), and with the comparable maximum size of the sicklefin devil ray *M. tarapacana* (340 cm DW) (Stevens et al., 2018). Furthermore, with the disappearance of the spinetail devil ray *M. japanica* from the roster of valid mobulid species (White et al., 2017), and with the tail spine being the most obvious and unique diagnostic feature of this species, we find it more sensible to propose that *M. mobular* inherit the common name of *M. japanica,* and henceforth be called the "spinetail devil ray" (Stevens et al., 2018), rather than extending the groundless name "giant devil ray" to all specimens formerly known as *M. japanica*.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s41200-020-00187-0.

Additional file 1 Measurements of *Mobula mobular*. Description of data: The file contains measurements of four specimens of *M. mobular*, and basic statistics of the sample are compared with statistics derived from the same measurements in a sample of 19 *M. japanica* (= *M. mobular*) from the Gulf of California, Mexico (Notarbartolo di Sciara, 1988).

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